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Food Selection and Nocturnal Behavior of the Land Snail *Monadenia hillebrandi mariposa* A. G. Smith (Pulmonata: Helminthoglyptidae)

by

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Abstract. Some aspects of the natural history of an endemic Californian snail, *Monadenia hillebrandi mariposa,* were studied. Analyses of feces and laboratory experiments were carried out to observe the food selection and nocturnal behavior of the animals. Larger animals tend to spend more time crawling, less time feeding, and travel longer distances than smaller ones, although larger animals exhibited high individual variability. The snails feed on both living and dead plant material. They have a broad diet, but seem to prefer certain food items, especially leaf litter. In this aspect they are similar to other terrestrial gastropod species reported in the literature.

INTRODUCTION

Little is known about the natural history and ecology of endemic Californian snails. The taxonomy of the western North American genus *Monadenia* has been extensively studied by Pilsbry (1939) and by Roth (1981), who divided the genus into three subgenera based upon shell morphology, reproductive anatomy, and area of distribution. One of these subgenera, *Corynadenia* Berry, 1940, occurs in California only and has long attracted the interest of malacologists and private shell collectors (Hanna & Smith, 1954). Recent collections of these snails indicate that various aspects of their ecology and evolution deserve further attention as well. Live specimens of some species were first found only a few years ago. Often, populations of the same species occur in isolated areas, resulting in a divergence of many morphological characters. This raises questions about their taxonomy, ecology, and evolution (Pressley, 1983; Roth, personal communication).

Monadenia (*Corynadenia*) *hillebrandi mariposa* A. G. Smith, 1957, has been found on limestone outcrops of the western foothills of the Sierra Nevada Mountains (Smith, 1957). It is a rock crevice dwelling species. Its yearly activity is restricted to a few months in the spring and fall. In the winter and summer the animals crawl deep into the cracks of the rocks and hibernate or aestivate respectively, thus avoiding the harshness of the physical environment. *Monadenia h. mariposa* is cryptic, hiding in crevices during the daytime and crawling on the surface only at night or on rainy days. Apart from these observations nothing is known of the feeding habits, nocturnal behavior, reproduction, or life history of the species. Based upon laboratory experiments and analyses of feces, this paper makes contributions to the natural history of the species, focusing on its diet and nocturnal behavior.

MATERIALS AND METHODS

Snails were collected during the night of 23 April 1982 from a limestone outcrop in the Stanislaus National Forest (California, Mariposa County, NW¼ sec. 29, T. 2 S, R. 18 E, Mount Diablo Base and Meridian, elevation: 800 m). All individuals collected were actively crawling and (or) foraging on the surface of the rocks. A total of 31 individuals (13 adults and 18 juveniles) was found. Snails with well-expressed lips were considered as adults. From the time of collection to the end of the experiments every individual was treated in the same way.

The snails were taken to the laboratory where they were weighed and their maximum shell diameter measured (Figure 1).

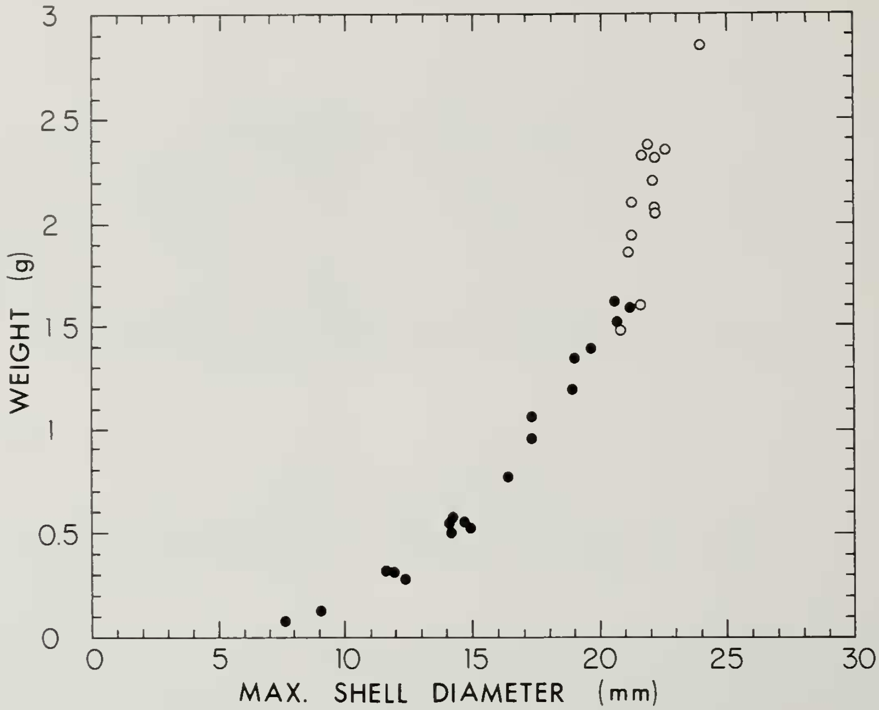

Figure 1

Relationship between maximum shell diameter and live weight of *Monadenia hillebrandi mariposa*. Filled circles, juveniles; open circles, adults.

Potential food resources in the form of living and dead plant material were also collected from the outcrop, and included the following. Living material: mosses (a mixture of *Grimmia trichophylla* Greville and *Rhytidiadelphus* sp.), a lichen (*Evernia prunastri* [L.] Acharius), *Selaginella hanseni* Hieronymus, grasses (a mixture of *Bromus tectorum* L. and *B. diandrus* Roth), an herb (*Phacelia imbricata* Greene), and pieces of limestone with algae growing on their surfaces. Dead material: bay litter (litter material only of *Umbellularia californica* [Hooker & Arnott] Nuttall), shrub litter (a litter mixture of buck rush, *Ceanothus cuneatus* [Hooker] Nuttall, service berry, *Amelanchier alnifolia* Munz, and interior live oak, *Quercus wislizenii* A. De Candolle), and pine litter (needle litter of digger pine, *Pinus sabiniana* Douglas).

Living plants and leaf litter accumulations were usually distributed in distinct patches in the field. Algae, mosses, and lichens were growing on rock surfaces.

In the laboratory, living plants were maintained in flower pots and the leaf litter was stored in plastic bags in a refrigerator.

The animals were kept in the laboratory at 13°C from 0700 to 1845 h, and at 10°C from 1845 to 0700 h at a 12L:12D photoperiod. They were fed with a dry cereal mixture of seven grains (wheat, barley, triticale, rice, rye, oats, and millet), which they readily accepted. Wet paper towels provided the necessary moisture. The animals were starved for 48 h before the onset of each experiment.

Laboratory Experiments

All the experiments were conducted in separate plastic boxes of 40 × 27 × 16 cm size. Excess amounts of the nine different food types were placed along the edges of the boxes. Observations on the behavior of the animals were made at night between 2000 and 0600 h. Each individual was checked every 20 min using a dim flashlight and its behavior was recorded. The experiments were conducted on three consecutive nights with each animal. Thus, a total of 90 records was made for each specimen.

Three categories (feeding, crawling, and resting) were used to describe the nocturnal activity of the snails. Hamilton & Wellington (1981b) and Newell (1966) used the same categories when observing the behavior of terrestrial slugs, although Newell also recorded mating behavior. This latter activity could be omitted in the present case, however, because the animals were kept individually.

Crawling distances were determined by tracing the snails' mucous trail with a marking pen on a plastic sheet placed over the top of each box. Trails on the sides and the lid of the box were also included. The total length of the trail was measured by using a map tracer. Crawling distances were measured during only one night for each animal.

The experiments were conducted during May 1982, a time of the year when snails were also active in the wild.

Analyses of Feces

To gain information about the natural diet of the animals, fecal analysis was carried out. Feces were obtained from the animals collected on 23 April 1982. Immediately after collection the snails were placed into individual containers lined with a wet paper towel to provide moisture. No food was given to the animals for 72 h. The feces produced during this time were collected from the boxes and microscopically examined. The animals, deprived of any other food source, started to rasp on the paper towel, which gradually appeared in their feces. Eventually the entire fecal material contained nothing but paper towel, mucus and (or) liver string. Feces without any trace of natural food were not included in the analysis.

The few samples of feces found in the field when the animals were collected were also analyzed.

Each sample was spread on microscope slides, covered with glycerine, and examined under a binocular microscope. The large particle size range and unidentifiable remnants prevented the quantitative evaluation used by Williamson & Cameron (1976), in which each component was given a score ranging between 0 and 10. However, the relative amounts of "green material" (including algae, moss, lichens, pieces of green leaves, *etc.*) and "brown material" (including leaf litter, senescent moss, lichen, herb leaves, pieces of twigs, and soil) were compared. Thus, the following seven categories were established based on the relative amounts of green and brown material:

- B = G if the brown:green ratio was 1:1
- B > G (and G > B) if the brown:green (green:brown) ratio was between 1:1 and 2:1
- B ≫ G (and G ≫ B) if the brown:green (green:brown) ratio was between 2:1 and 5:1
- B >>> G (and G >>> B) if the brown : green (green : brown) ratio was greater than 5:1.

Digestive gland feces (liver string), which consist of fine brown particles originating from intracellular digestion, were not included in this evaluation.

RESULTS

Nocturnal Activity in the Laboratory

Twenty-eight animals emerged and were active (that is, spent most of their time feeding and [or] crawling) during all three nights. The three individuals that behaved differently were mostly resting or did not emerge at all. It is possible that they suffered some damage during collecting or handling in the laboratory. However, it is also possible that this is normal. In Richardson's (1975) experiments 80% of the snail population was active each night.

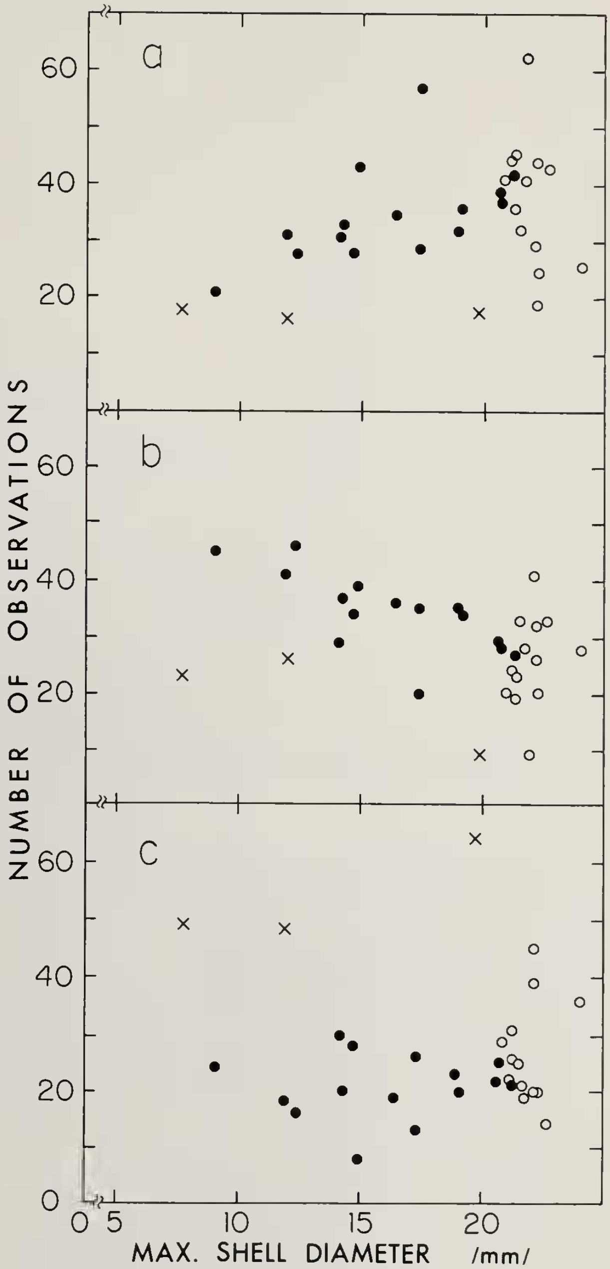

Figure 2

Relationship between size and three types of activity of *Monadenia h. mariposa*. a, crawling; b, feeding; c, resting. Filled circles, juveniles; open circles, adults; crosses, individuals that were not active each of the three nights.

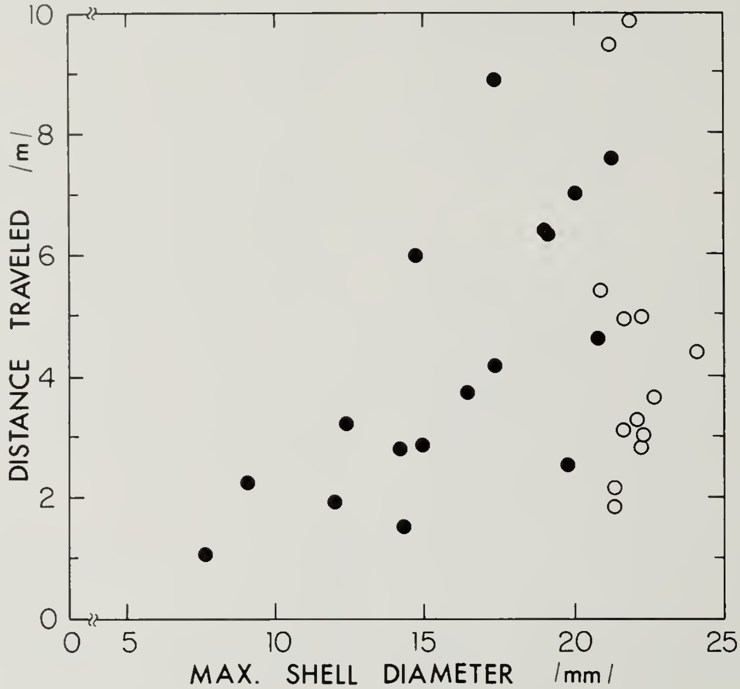

Figure 3

Relationship between size and crawling distances of *Monadenia h. mariposa.* Filled circles, juveniles; open circles, adults.

The active snails were either crawling or feeding. They moved not only among food items but often crawled on the walls and the tops of the boxes as well. The snails frequently followed their own slime trails. Looped paths were also observed. These behaviors can be associated with orientation, although trail following may also lower energetic costs by reducing the mucus production needed for movement (ROLLO & WELLINGTON, 1981; HALL, 1973). The snails frequently lifted their heads and waved their tentacles, indicating that *Monadenia h. mariposa* may also use olfactory cues to orient.

The moving and feeding activities were interrupted by periods of rest that varied in length between a few minutes and hours. During long resting periods the animals often defecated.

The scores (numbers of observations of each individual during the three nights) for each type of activity are shown in Figure 2. There was a positive correlation ($r_s = 0.34$, $P < 0.05$, Spearman rank correlation test) between size and crawling scores, and a negative one ($r_s = -0.36$, $P < 0.05$) between size and feeding scores. The correlation, however, was weak in both cases. This was mostly due to the high variation of scores for adults. There was no significant correlation between maximum shell diameter and resting scores. The correlation between feeding and crawling scores was not significant either.

When the activities of adults and juveniles were compared, only the feeding scores yielded a significant difference (Mann-Whitney U test, two-tailed).

Crawling distances (Figure 3) varied between 1 and 10 m per night. The range of the values for the adults again was large. The correlation coefficient ($r = 0.37$) was still significant at the 0.05 level. For juveniles only the correlation coefficient was much higher ($r = 0.68$, $P < 0.01$). Crawling distances were measured only one night with each individual.

Food Selection in the Laboratory

Figure 4a shows the total number of times animals were observed feeding on each food type. Although the snails accepted many different kinds of food, they were clearly selective ($\chi^2 = 268.9$, $P < 0.001$). Shrub and bay litter were ranked first and second respectively. The animals were frequently observed rasping on the xylem parts of small twigs. Grass and pine litter were the least selected.

The food selection of adults and juveniles (Figure 4b) was significantly different ($\chi^2 = 47.60$, $P < 0.01$). This, however, was entirely due to the difference between scores given for the stones with algae. If this category, which was ranked seventh when all scores were combined, were excluded from the χ^2 test, then there was no significant difference between the food selection of adults and juveniles.

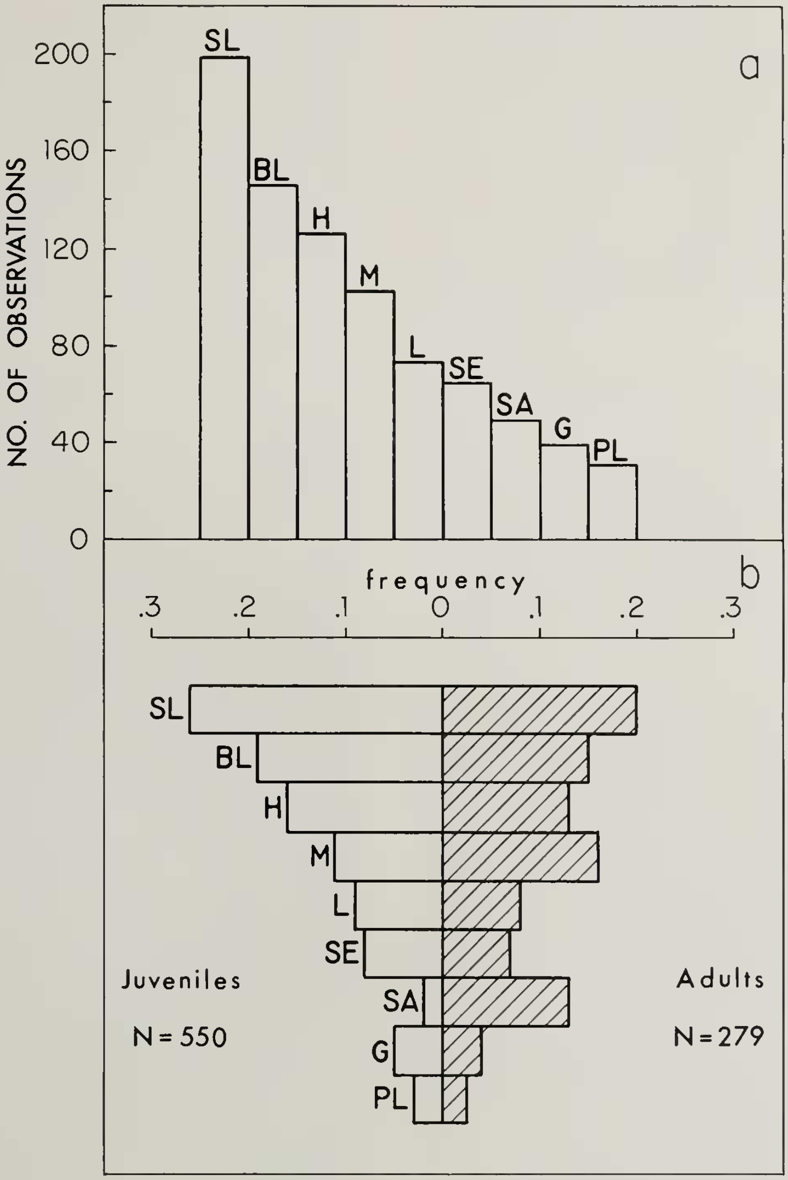

Figure 4

Food selection of *Monadenia h. mariposa* in the laboratory. a. All data combined. b. Adults and juveniles separately. Abbreviations: SL, shrub litter; BL, bay litter; H, herb; M, moss; L, lichen; SE, *Selaginella*; SA, stone with algae; G, grass; PL, pine litter.

Analyses of Feces

A total of 135 samples of feces was examined. Of these, 34 samples were disregarded, as they contained nothing but digestive gland feces, mucus, and (or) paper towel, indicating that the gut was empty. The remaining 101 samples were then analyzed mostly qualitatively. These contained food items the snails had selected in their natural habitat. Attempts were made to identify only the moss and lichen components. The ones that could be determined at least to genus level included the mosses *Rhytidiadelphus* sp. and *Grimmia trichophylla* Greville, and the lichens *Leptogium* sp. and *Physcia* sp.

The results (Figure 5a) showed that, although most of the samples contained green and brown material, the latter highly dominated in the feces ($\chi^2 = 45.76$, $P < 0.001$).

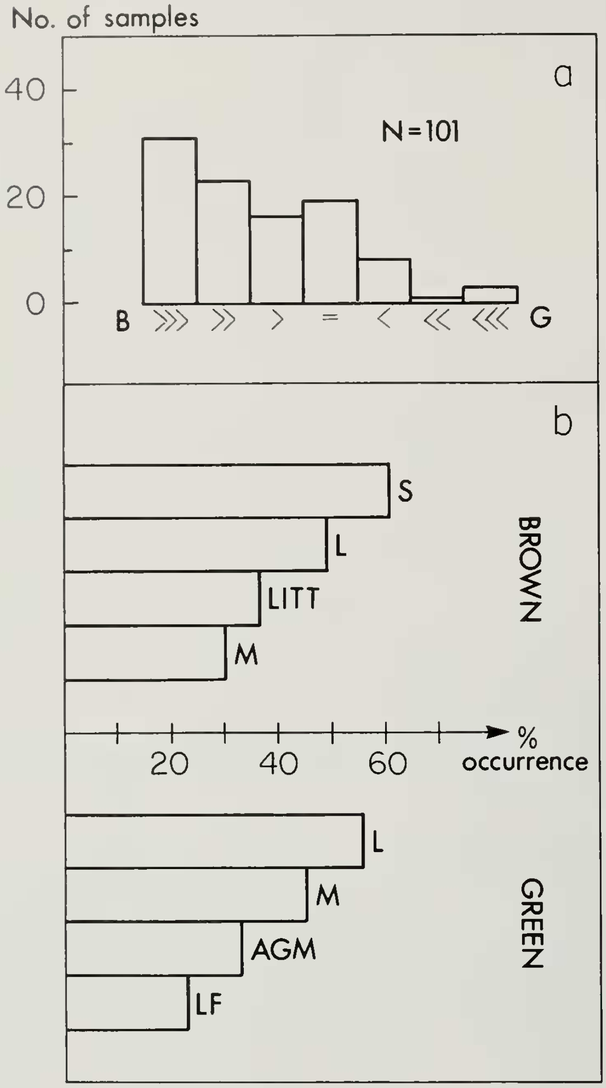

Figure 5

a. Comparison between the brown and green parts of the feces of *Monadenia h. mariposa*. See "Methods" for explanation of each category. b. The percentage occurrence of the major components in the fecal material. Abbreviations: S, soil; L, lichen; LITT, litter material, senescent leaves; M, moss; AGM, amorphous green material; LF, leaf fragments of higher plants.

The percentage occurrence of different food types is given in Figure 5b. Lichens were highly ranked in both the brown and green categories. Soil occurred in 61% of the samples and its relative amount was also high. In 12 samples the entire feces contained nothing but soil. The occurrence of white mineral particles (either quartz or limestone) was also high (47%).

Other plant material not shown in Figure 5b included (the number of samples are given in parentheses): flower remnants (1) and seeds (2). The following animal matter was also found in a few samples: insect wings (2), a coleopteran thorax and leg (1), pieces of radula (2), and white spherical material that looked like eggs (6).

Digestive gland feces ("liver string") was found together with gut feces in only 28 samples. In the other cases in which it occurred, the feces contained only paper towel or mucus (the 34 disregarded samples). This supports RICHARDSON's (1975) finding that intracellular digestion, which results in liver string production, becomes more important in the metabolism of the snails when they feed on food of low digestibility or starve.

DISCUSSION

The results in Figures 2a and 3 indicate that larger animals tend to crawl more (that is, they spend more time crawling and travel greater distances) than smaller ones. VAN DER LAAN (1971) found that larger specimens of *Helminthoglypta arrosa* moved farther than smaller ones. In the experiments of HAMILTON & WELLINGTON (1981a), dispersing individuals of *Arion ater* were significantly heavier than non-dispersers, although this was not the case for large-bodied *Ariolimax columbianus*. Larger animals may have relatively larger stored energy reserves (HEATWOLE & HEATWOLE, 1978) and, therefore, may be able to travel greater distances than smaller ones. They are also more likely to survive unfavorable conditions. In a study investigating Puerto Rican camaenid snails, HEATWOLE & HEATWOLE (1978) found that the survival of adult *Caracolus carocollus* during dry periods and food shortages was much higher than that of the juveniles. VAN DER LAAN (1975b) also reported that the smallest individuals of *Helminthoglypta arrosa* suffered the highest mortality under dry conditions. It is the individuals of larger and, therefore, less vulnerable size that may be responsible for the dispersal of a population. It is also possible that larger animals have larger home ranges. More information is needed about the homing behavior and dispersability of *Monadenia* to resolve the problem. Small individuals probably have to spend more time feeding, especially because the active period of the population is strongly restricted by climatic factors throughout the year.

The nocturnal behavior of *Monadenia h. mariposa* shows high individual variability. It is particularly remarkable among adults that are of similar size. In their case it may be related to various activities of reproduction (searching for mates, egg production, *etc.*). Long-term studies of movement by other species of snails have also shown high variability among individuals in distances traveled (*Helminthoglypta arrosa*: VAN DER LAAN, 1971; *Littorina irrorata*: HAMILTON, 1978). LOMNICKI (1969), studying adult members of a *Helix pomatia* population, distinguished between "wide ranging" and "narrow ranging" individuals in terms of their mobility. In the present study the small sample size prevented any attempt to determine a frequency distribution for the different types of activity.

From both the feeding experiments and the analyses of feces it is obvious that *Monadenia h. mariposa* is neither an obligate herbivore nor a detritivore, although dead plant material comprises the majority of its diet. Most studies investigating terrestrial gastropod diets agree that snails and slugs consume fresh as well as dead plant material (*e.g.*, BOYCOTT, 1934; CHATFIELD, 1976; JENNINGS & BARKHAM, 1975; WOLDA *et al.*, 1971), but many of these gastropods have strong preferences for certain types of dead plant material (*e.g.*, RICHARDSON, 1975; VAN DER LAAN, 1975a; CHATFIELD, 1976; MASON, 1970).

There are two major factors that may determine the acceptance of a plant material once encountered: texture and taste. For snails the most important components of the former are the "roughness" and the "toughness" of the external surface. As in the findings of GRIME *et al.* (1968) for *Cepaea nemoralis*, epidermal hairs have no influence on the acceptance of certain food items by *Monadenia h. mariposa*. The herb *Phacelia imbricata* is densely covered with hairs and yet ranked third in the feeding preference. Hairy plant remnants were found in the fecal samples as well. Although *Selaginella hanseni* ranked only sixth, the spines on the tips of the leaves did not protect them from being eaten, and the snails easily crawled across the plant. GRIME *et al.* (1968) also found that hard external surfaces act as a barrier for *Cepaea nemoralis*. In the present investigation *M. h. mariposa* was never observed rasping on the leathery leaves of interior live oak that were in the shrub litter. *Monadenia setosa* Talmadge, a closely related species, also refused oak-leaf litter which is part of its natural substrate (ROTH & ENG, 1980), and oak leaves were not consumed by most of the slug species studied by JENNINGS & BARKHAM (1975). Oak leaves are also known to contain a high percentage of tannins that act as a defensive agent against herbivory (FEENY, 1970; SATCHELL & LOWE, 1967). This may be another reason why *M. h. mariposa* refused to feed on them.

The high rank of the bay litter is somewhat surprising. The bay tree produces essential oils. The exact role of these aromatic compounds is not known, although according to KRAMER & KOZLOWSKI (1979), they may be important in attracting pollinators or repelling herbivores. The only other study in which a gastropod was reported utilizing California bay laurel as a food source is that of INGRAM & HAND (1949), who observed the slug *Ariolimax columbianus* feeding on the fruit of the bay tree.

Grasses were generally refused by *Monadenia h. mariposa*. This is in agreement with most of the studies investigating snail diet (RICHARDSON, 1975; WOLDA *et al.*, 1971; VAN DER LAAN, 1975a; INGRAM & PETERSON, 1947). One exception is the study by WILLIAMSON & CAMERON (1976), in which *Cepaea nemoralis* ate some grass, consisting mostly of senescent blades. The grass and pine litter, which were least selected, were found on the edges of the outcrop. Often it is grassland that separates the limestone outcrops on which snail populations occur.

It is difficult to understand the diets of terrestrial gastropods, because little is known about their nutritional needs. Nonetheless, CHATFIELD (1973), WILLIAMSON & CAMERON (1976), and RICHTER (1976) reported the highest growth rate of juvenile gastropods on a mixed diet. Snail diets may certainly change due to seasonal availability of food types (CHATFIELD, 1976; WILLIAMSON & CAMERON, 1976; WOLDA *et al.*, 1971; VAN DER LAAN, 1975a; RICHTER, 1979). Also, in the case of *Monadenia h. mariposa*, diet probably depends on the local food availability, which may differ on the various limestone outcrops.

The analysis of feces, which reflects food choice in the natural habitat, resulted in a higher rank of certain food items, especially lichens and algae, as compared to the laboratory observations on the food selection by *Monadenia h. mariposa*. This, and the high occurrence of white particles in the feces, indicate that the animals may readily rasp anything they encounter on the surface of the rocks. GRIME & BLYTHE (1969) reported that the feces of *Helicigona lapicida* and *Cepaea nemoralis* individuals collected from limestone outcrops contained a large proportion of lichens.

The very few cases in which animal matter was found in the feces seem to be the result of accidental ingestion as has been found in other studies (WILLIAMSON & CAMERON, 1976; RICHARDSON, 1975; WOLDA *et al.*, 1971; HEATWOLE & HEATWOLE, 1978).

The frequent occurrence of the soil in the feces is somewhat surprising. It is not known how snails utilize it, although several hypotheses have been put forward concerning soil as a "grinding agent" (STOREY, 1970), a calcium source, or a food source (WILLIAMSON & CAMERON, 1976). The first hypothesis seems unlikely for *Monadenia h. mariposa*. It would be difficult to explain the large (sometimes 100%) amount of soil in the feces if its function were solely to help break up plant material. It is possible, however, that snails are able to extract some nutrients, or utilize the microorganisms that live in the soil. Soil seems to be an important food source for the land snail *Helicella virgata* as well. POMEROY (1969) has found that this snail in South Australia mostly feeds by scraping the surface of the topsoil.

Because of the broad diet and the usually abundant food supply, many authors think that food is not an important factor determining either the occurrence or the density of terrestrial gastropods (BOYCOTT, 1934; WOLDA *et al.*, 1971; WILLIAMSON & CAMERON, 1976). The snail population of the south-facing slope of the Winnats Pass in Derbyshire, England, where a large proportion of the limestone is exposed bare surface, is an exception. The density of the snail population there appears to be limited by food (GRIME & BLYTHE, 1969). Clearly, long-term field observations and experiments are necessary to clarify the situation in the case of *Monadenia h. mariposa* and other related snails.

In summary, for the habits investigated in this study, *Monadenia hillebrandi mariposa* fits fairly well into the general picture we have about terrestrial gastropods. Their nocturnal behavior is similar to what has been described for other snail and slug species. They have a broad diet but still show selectivity. They feed on both living and dead plant material, but tend to prefer the latter.

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